Global hotspots and correlates of alien species richness across taxonomic groups

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Human-mediated transport beyond biogeographic barriers has led to the introduction and establishment of alien species in new regions worldwide. However, we lack a global picture of established alien species richness for multiple taxonomic groups. Here, we assess global patterns and potential drivers of established alien species richness across eight taxonomic groups (amphibians, ants, birds, freshwater fishes, mammals, vascular plants, reptiles and spiders) for 186 islands and 423 mainland regions. Hotspots of established alien species richness are predominantly island and coastal mainland regions. Regions with greater gross domestic product per capita, human population density, and area have higher established alien richness, with strongest effects emerging for islands. Ants and reptiles, birds and mammals, and vascular plants and spiders form pairs of taxonomic groups with the highest spatial congruence in established alien richness, but drivers explaining richness differ between the taxa in each pair. Across all taxonomic groups, our results highlight the need to prioritize prevention of further alien species introductions to island and coastal mainland regions globally.

The transport of species across biogeographic barriers by humans is a key component of global environmental change[1-3]. Some of the species introduced to new regions will establish self-sustaining populations and, thus, become a persistent part of the local biota[4]. Numbers of these established alien species (hereafter EAS) are predicted to increase further as a result of increasing global trade, land-use intensification, urbanization and climate change[5]. Whilst patterns of EAS richness have been analysed for particular regions[6-8] and taxa[9-13] individually, we still lack a global synthesis across a broad range of taxonomic groups. Such a synthesis will be invaluable for identifying (i) geographical hotspots and coldspots of EAS richness, both across

and within taxonomic groups, and for (ii) identifying and assessing potential correlates and drivers of EAS richness across different taxonomic groups

Here, we assess global patterns and correlates of EAS richness across eight taxonomic groups by integrating comprehensive published (vascular plants[12], birds[13], fishes[14] , ants[15], spiders[16]) and so far unpublished databases (amphibians, mammals, reptiles) (Fig. 1). As a spatial framework, we use the 609 regions (186 islands/archipelagos and 423 mainland regions) from level 4 of the Biodiversity Information Standards framework (TDWG) [17], representing countries or states and provinces within larger countries, and major islands and archipelagos. We identify the global hotspots (high richness) and coldspots (low richness) of EAS across the taxonomic groups while accounting for differences in area and sampling effort. Sampling effort consists of published inventory completeness estimates of native species of amphibians, birds and mammals[18], vascular plants[19] and native genera of ants[20] as a proxy (see methods). We also explore additional macroecological and socioeconomic correlates behind cross-taxon EAS richness patterns.

We expect regions with higher gross domestic product per capita (GDPpc) or with higher population densities to receive more alien species introductions across taxa (i.e., to experience higher colonisation pressure through trade and transport), resulting in higher EAS richness[7,8,10,21]. We also test whether EAS richness patterns follow the latitudinal gradients often observed for native biota, with higher richness in regions with higher mean annual temperature and precipitation[22,23]. We expect island regions to have higher EAS richness than mainland regions, as islands are thought to be more prone to the establishment of alien species[12,24,25]. In addition, we expect more isolated oceanic islands to have greater EAS richness, as they have been shown to receive more introductions, at least for birds[9]. We also expect coastal regions (as points of

105 introduction) to have higher EAS richness than landlocked regions. Finally, we assess the degree
106 of spatial congruence of EAS richness among taxonomic groups and explore the variables that
107 might explain differences in spatial species-richness patterns among groups.

108

109 **Results**

110 *Established alien species richness and its drivers*

111 After accounting for area and sampling effort, hotspot regions for EAS richness across
112 taxonomic groups are predominantly islands, with the top three regions being the Hawaiian
113 Islands, New Zealand's North Island and the Lesser Sunda Islands (Indonesia) (Fig. 2;
114 Supplementary Table 1). The top three coldspots are Antarctica (unsurprisingly), Coral Sea
115 Island Territory (Australasia) and Laccadive Islands (Supplementary Table 1). Representation of
116 continents differs markedly for regions above and below the richness median ($\chi^2 = 16.34$, df = 8,
117 $P = 0.04$), with the Pacific Islands, Europe and Australasia represented disproportionately among
118 higher-richness regions (Fig. 2; Supplementary Table 2). The model best explaining cross-taxon
119 EAS richness for mainland and island regions includes GDPpc, population density and sampling
120 effort, as well as area, mean annual precipitation, and whether a region is mainland or island(s)
121 (Supplementary Table 3; Table 1). Following the (almost) universal species-area relationship for
122 native species, larger regions have higher EAS richness, but regions with greater GDPpc, higher
123 population density and greater sampling effort for native flora and fauna also have higher EAS
124 richness (Table 1). The effects of climate are less pronounced than those of area, GDPpc and
125 human population density, with a weak trend of higher alien richness in wetter regions (Table 1).
126 While we only have potential proxy data (GDPpc, population density) for colonisation pressure
127 here (i.e., the total numbers of species introduced)[26], our results suggest that cumulative numbers

of EAS are driven to a greater extent by differences in area and the pressure of introductions from human history and activity[1,3,5,12,21] than by climate.

Island regions have on average higher cross-taxon EAS richness (mean ± 1 S.D. proportional cross-taxon richness = 0.17 ± 0.11) than mainland regions (mean ± 1 S.D. = 0.11 ± 0.07; Table 1). In addition, models explaining alien richness of island and mainland regions separately reveal that EAS richness is more strongly related to area, GDPpc and population density on islands than in mainland regions (Table 1). Moreover, EAS richness is strongly related to mean annual temperature for islands, with warmer regions having higher richness, while the effect of mean annual temperature on mainland region richness was reversed, with cooler regions having higher richness (Table 1). Mainland regions with better sampled native species also harbour more EAS, but for island regions the effect of sampling effort is weaker (Table 1). Among mainland regions, EAS richness is greater for coastal (mean ± 1 S.D. proportional cross-taxon richness = 0.13 ± 0.09) than for landlocked regions (mean ± 1 S.D. = 0.10 ± 0.04). Cross-taxon EAS richness on islands tends to be higher for those further from continental landmasses (Table 1).

Taxonomic congruence

The strongest correlations in alien richness between taxonomic groups exist for ants and reptiles (r_s = 0.62), followed by birds and mammals, and vascular plants and spiders (both r_s = 0.55) (Table 2). For ants and reptiles, EAS richness is high in the Hawaiian Islands, southern United States (especially Florida) and Madagascar and the Mascarene Islands (Fig. 1b, 1g). Mammals and birds both have high EAS richness in New Zealand, Hawaiian Islands, Florida and California, and are less congruent in Australia, Western Europe and the Caribbean (Figure 1c,

1e). Alaska, British Columbia and southern Africa tend to have high EAS richness of mammals, but not birds (Figure 1c, 1e). Plants and spiders both have high EAS richness in Hawaii, California and Florida, but are less congruent in other coastal regions of the USA and Canada, and in Australia (Fig. 1f, 1h). In Europe, the United Kingdom has the highest established alien plant richness, while Germany has the highest spider richness (Fig. 1h, 1h). Overall, the Hawaiian Islands, California, Florida and Australasian regions stand out as having high EAS richness for multiple taxonomic groups (Fig. 1).

The strong correlation in EAS richness between ants and reptiles is reflected in the positive relationship between mean annual temperature and EAS richness of these two taxonomic groups (Fig. 3). For both plants and spiders, human population density shows a strong positive relationship with EAS richness. However, the effects of socioeconomic and macroecological drivers on EAS richness differ markedly between birds and mammals despite the strong correlation between them, with stronger sampling effort effects for birds (Fig. 3). In addition, EAS richness of fishes, mammals and plants is negatively related to mean annual temperature, despite the relatively weak correlations among them (Fig. 3; Table 2). All other drivers included in best-fitting (lowest AICc) models for each taxonomic group have a positive relationship with EAS richness (Fig. 3).

Discussion

Our results show that, per unit increase in area, GDPpc, and population density, EAS richness increases at a faster rate in island than in mainland regions. A potential reason may be that island regions are more readily invaded by alien species than mainland regions[25], although a rigorous test of this explanation would require data on failed introductions[26]. The opposing

174 relationships between mean annual temperature and richness for island and mainland regions
175 may result from geographical bias in human activities for islands. Many economically
176 independent island states are tropical, and may have high foreign import volumes (and thus high
177 colonisation pressure), whereas most non-tropical islands are part of larger mainland states, with
178 presumably limited foreign trade (and thus low colonisation pressure). The opposite may explain
179 the lower EAS richness in tropical mainland regions, which have smaller trade volumes than
180 temperate mainland regions[5]. Higher EAS richness in coastal than landlocked mainland regions
181 is likely to be a consequence of the presence of ports in coastal regions[1], resulting in overall
182 greater rates of species introductions, as previously shown globally for birds[13] and for multiple
183 aquatic species in the UK and Ireland[27]. Despite these effects, substantially more variation (20-
184 26% more) in EAS richness is explained when also accounting for continent and subcontinent
185 effects (marginal vs. conditional R^2, Table 1). This indicates that EAS richness may be further
186 driven by spatially correlated socioeconomic, historical or political factors not captured by the
187 variables analysed here. For example, some countries with high per-capita GDP have recently
188 adopted biosecurity regulations to prevent introductions [13], while the global spread of the tropical
189 fire ant (*Solenopsis geminata*) originates from accidental introductions during European
190 colonialism[28]. Such historical and political effects will drive fine-scale variation in colonisation
191 pressure[26], which has been shown to be the strongest determinant of alien bird species richness
192 globally[13], and for which the socioeconomic information used here may not be a strong proxy.

193 The moderate-to-strong correlations in EAS richness between birds and mammals, plants
194 and spiders, and ants and reptiles may indicate that EAS richness patterns of these pairs of taxa
195 share similar underlying drivers. Indeed, the models best explaining ant and reptile richness
196 include strong positive effects of mean annual temperature on alien richness (Fig. 3). The

197 correlation between plant and spider richness may reflect horticulture and fruit/vegetable imports
198 acting as major pathways of accidental introductions for both groups[29]. Human population
199 density has similarly strong effects on richness for plants and spiders, but also for fishes,
200 potentially reflecting a greater number of introductions for these groups that have occurred in
201 more densely populated regions (Fig. 3).

202 However, spatial congruence of EAS richness may also result from different underlying
203 drivers. For instance, mean annual temperature has a negative effect on established alien plant
204 richness, but is not retained in the model for spider richness (Fig. 3). Similarly, while cooler
205 regions have higher established alien mammal richness, possibly reflecting more frequent
206 transfers of mammals between temperate regions[30], temperature is unimportant for explaining
207 established alien bird richness (Fig. 3) despite the strong congruence in the richness of these
208 taxa. While some taxonomic groups show higher spatial congruence than others, no pairwise
209 correlation is above 0.6, in contrast to native species richness[31]. This indicates that there is a
210 substantial amount of spatial variation in EAS richness among groups (Fig. 1), and as such the
211 effects of key macroecological and socioeconomic correlates will also vary (Fig. 3).

212 Sampling effort is much more strongly related to established alien bird than to mammal
213 richness, despite their positive correlation (Fig. 3). Historical introductions of birds occurred
214 through pet trade and Acclimatization Societies[13,32,33] and may be tightly linked to sampling
215 effort (regions with the best record of native bird richness also tended to have more alien
216 birds)[13]. Ultimately, completeness of regional inventories, and introduction and recording of
217 alien species could be driven by similar historical, socioeconomic or cultural factors. For
218 instance, regions that have channelled more resources towards creating a more complete record
219 of native species may be the same ones importing and recording more alien species. However,

220 the extent to which current per-capita GDP and population density reflect colonisation pressure
221 and sampling effort in the past is likely to differ among taxa.

222 Our global assessment of EAS richness and its correlates across eight different taxonomic
223 groups reveals that island regions across the globe, relative to their size and sampling effort,
224 harbour consistently more alien species than mainland regions. Densely populated islands with
225 higher GDPpc and with warmer climates are particularly vulnerable. Coastal mainland regions
226 also have higher EAS richness than landlocked ones. Island and coastal mainland regions may be
227 alien species hotspots because colonisation pressure is higher, as has been shown for birds[13], or
228 because establishment rates among introduced alien species is higher in these regions. Across
229 multiple taxa, it remains to be tested which of these two possibilities is more likely.
230 Socioeconomic factors are clearly important for explaining EAS richness for all taxonomic
231 groups, but effects vary depending on the group under study. This likely reflects differences
232 among taxonomic groups in how well socioeconomic activity reflects colonisation pressure.
233 Ultimately, data on the failed introductions, as well as the successful ones, will enable us further
234 to understand global patterns in EAS richness. Nonetheless, the types of regions most vulnerable
235 to EAS that we have identified should be considered priorities for efforts aimed at preventing
236 further species introductions.

237

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and S-L.S for mammals, and W.N. for spiders. D.M. collected and calculated data on region area and sampling effort. C.M. contributed data on completeness of native species richness inventories.

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Figure 1 | Established alien species richness in the 609 TDWG level-4 regions with data available per taxonomic group. a) amphibians, b) ants, c) birds, d) freshwater fishes, e) mammals, f) vascular plants, g) reptiles and h) spiders. Grey areas represent regions with no data available for a particular taxonomic group. Scales indicate numbers of species.

Figure 2 | Hotspot and coldspot regions for cross-taxon established alien species richness across eight taxonomic groups (amphibians, ants, birds, freshwater fishes, mammals, vascular plants, reptiles and spiders), accounting for area and sampling effort. Only TDWG level-4 regions (i.e. countries, federal states and islands/archipelagos) with data on sampling effort available were included (n=534). Cross-taxon established alien species richness of grey-bordered regions was calculated from three or fewer taxonomic groups, and of black-bordered regions from four or more taxonomic groups. Cross-taxon established alien species richness comprises residuals from a linear model, ln[cross-taxon alien richness]~ln[Area] × sampling effort. Upper and lower 2.5% and 10% regions are indicated separately from the remaining upper and lower 50% regions.

Figure 3 | Effects of area, climate, sampling effort, GDP per capita, human population density and whether a region is coastal on established alien species richness of eight taxonomic groups (mainland regions only, due to insufficient data for islands for all taxonomic groups). Estimates (± 1 standard error) of effects were obtained from linear mixed effects models of ln(species richness+1), with regions, nested in subcontinental regions (TDWG level 2) and continents as random effects. Note that only variables that were kept in the final models are shown (Supplementary Table 6), thus numbers of estimates differ between groups. Numbers in parentheses are numbers of regions included per taxonomic group.

Table 1 | Estimates of models explaining cross-taxon established alien species richness for all regions, and for mainland or island regions only. Cross-taxon alien richness was natural-log transformed, as were GDP per capita (thousands $US), human population density (10^3 people km^{-2}) and region area (km^2). Mean annual precipitation (MAP) was square-root transformed. Standard errors are in parentheses. Random effects of TDWG level 2 regions and continents and residual variation (italics) are shown as 1 standard deviation. Shaded cells indicate when a variable was not considered. Marginal R^2 (variation explained by fixed effects) and conditional R^2 (fixed and random effects) are also given.

	All regions	Mainland	Island
N	446	371	75
Intercept	-1.74 (0.08)	-2.32 (0.05)	-1.92 (0.10)
Area	0.35 (0.03)	0.25 (0.02)	0.53 (0.07)
Sampling Effort	0.17 (0.03)	0.17 (0.03)	0.10 (0.06)
Area × Sampling Effort	0.07 (0.02)	0.08 (0.01)	
Mainland	-0.44 (0.07)		
Coastal		0.13 (0.03)	
Distance to continent			0.18 (0.07)
MAT		-0.08 (0.03)	0.25 (0.10)
MAP	0.06 (0.02)	0.06 (0.02)	
GDP per capita	0.19 (0.03)	0.12 (0.03)	0.31 (0.07)
Human Population density	0.23 (0.02)	0.19 (0.03)	0.35 (0.07)
TDWG continent	*0.14*	*0.07*	*0.22*
TDWG L2 region	*0.24*	*0.20*	*0.31*
Residual	*0.30*	*0.26*	*0.40*
Marginal/Conditional R^2	0.45/0.71	0.49/0.69	0.58/0.79

Table 2 | Established alien species richness correlations (Spearman's r_S) between pairs of the eight taxonomic groups, for all regions with data available. Significant ($P < 0.05$) correlations are indicated in bold.

	Ants	Amphibians	Mammals	Birds	Fishes	Plants	Spiders
Reptiles	**0.62**	**0.41**	**0.26**	**0.44**	**0.14**	**0.17**	**0.34**
	Ants	**0.34**	0.10	**0.29**	**0.15**	0.06	**0.28**
		Amphibians	**0.43**	**0.47**	**0.19**	**0.19**	**0.34**
			Mammals	**0.55**	**0.23**	**0.32**	**0.36**
				Birds	**0.34**	**0.39**	**0.46**
					Fishes	**0.35**	**0.40**
						Plants	**0.55**

372 **METHODS**

373 **Data compilation.** Data on established alien species (EAS) richness were obtained from
374 databases for eight taxonomic groups (amphibians, ants, birds, mammals, vascular plants,
375 reptiles, spiders). The data on amphibians, reptiles and spiders, and fishes in some regions were
376 compiled specifically for this study. For all taxonomic groups, only EAS outside of their native
377 ranges have been considered.

378 Data on alien vascular plants were obtained from the Global Naturalized Alien Flora
379 database version 1.1[12], a recently compiled database including 13,168 plant species (including
380 hybrids and subspecies). The data consists of lists of established alien plant species in 843
381 geopolitical regions, largely conforming to countries, states, provinces and counties within
382 countries, as well as islands and archipelagos. Data on established alien ants were obtained from
383 the Global Ant Biodiversity Informatics project database, which consists of geographical records
384 of species' presences (accessible through antmaps.org[15]). Only species records representing
385 establishment in the wild (e.g. not in glasshouses or buildings) were included, amounting to 4061
386 records for 237 species in total. Data on established alien bird species were obtained from the
387 Global Avian Invasions Atlas[31], which is a comprehensive global database of 971 alien bird
388 species with 27,723 introduction records at a 1-degree grid-cell resolution. Data on 445
389 established alien mammal species were obtained from a geographically complete mammal
390 database (Alien Mammal Data v1.0), which contains records of established alien mammal
391 species in global administrative areas (GADM; www.gadm.org). Data on 81 established alien
392 amphibian and 203 established alien reptile species were compiled from multiple sources into a
393 database, the Global Alien Amphibians and Reptiles Database, by Capinha, Essl and Seebens
394 specifically for the purpose of this study, and merged with a separate database compiled by
395 García-Díaz. Data on 454 established alien freshwater fish species (including migratory species

with marine life-stages, a total of 2968 records) were taken from the FishBase database[14] (accessed 13th of October 2015), and supplemented for the U.S.A. with the U.S. Geological Survey's Nonindigenous Aquatic Species database (compiled by Fuller), Canada (compiled by Mandrak), multiple sources for Mexico[32], Argentinian, Chilean, Australian, New Zealand[33,34] and South African provinces (compiled by García-Berthou)[35,36], Japan[37] and Brazil[38]. Finally, 2138 records on 207 established alien spider species were compiled via a comprehensive literature search by Nentwig, including the World Spider Catalog[16] as a major source, and literature available therein.

Because the data for the different taxonomic groups came from different sources and were originally collected at different spatial resolutions, we harmonised all data sets to fit within the Biodiversity Information standards (TDWG) geographic system[17]. This hierarchical system includes as the finest spatial resolution (Level 4) a layer of 609 regions, mostly comprising countries, states and provinces of larger countries and major island groups. Species records for each taxonomic group were assigned to TDWG level 4 regions, and the total number of EAS per taxonomic group within each region was calculated. Global data coverage was highest for birds and mammals (both have all 609 regions), followed by vascular plants (449 regions, 82% of global ice-free terrestrial area), ants (402 regions, 64% of area), freshwater fishes (363 regions, 70% of area), spiders (348 regions, 66% of area) and, lastly, amphibians and reptiles (311 and 310 regions, 48% and 47% of area, respectively).

Estimating sampling effort. Variation in sampling of EAS among regions can bias the perceived global patterns in alien species richness. However, data directly measuring the degree of sampling effort of EAS recorded in each region are not available. To account for this potential

bias, we instead estimated sampling effort for native species of five taxonomic groups: amphibians, ants, birds, mammals and vascular plants. For amphibians, birds and mammals, we obtained global data at a 12321 km^2 (~1 degree) grid cell resolution, comprising the percentage completeness of native species inventories for these groups based on occurrence records mobilized *via* the Global Biodiversity Information Facility (GBIF)[18]. For vascular plants, we obtained data[19] at the same resolution comprising the percentage completeness of species records in GBIF, as assessed through comparison with independent estimates of native vascular plant richness. For ants, we used region estimates of the percentage of native ant genera missing from records in the Global Ant Biodiversity Informatics project database (these estimates were obtained from models predicting ant diversity and endemicity, and region completeness was calculated as 100 per cent minus the percentage of missing genera)[20]. We then calculated the average completeness across grid cells for each TDWG level 4 region large enough to overlay the majority of at least one grid cell (534 regions in total: completeness could not be calculated for 64 island and 11 mainland regions). An average completeness value across the five taxonomic groups was then calculated per region, and used in subsequent analyses of cross-taxon alien richness (see below; Supplementary Fig. 1). When a taxonomic group had native completeness data available, this was used in the single taxon analyses (see below). Correlations between completeness values for individual taxonomic groups are all significantly positive (Supplementary Table 4), and as vertebrates, invertebrates and vascular plants are included, we are confident that the average completeness across these groups is broadly representative of the missing three taxonomic groups.

Our use of native species inventories as a proxy for sampling effort of EAS recording assumes there is a linear positive relationship between sampling efforts of alien and of native

species. However, the completeness measures are based on data sources which also include records of alien species, and we have no reason to believe that addition of EAS records will differ spatially in a fundamentally different way from native species records. By focusing our sampling effort estimates on native species, we ensure greater statistical independence between the estimates of EAS richness and sampling effort. In addition, completeness of regional inventories and recording of EAS could be driven by ultimately the same factors, such as human history, socioeconomy and culture. So we may expect certain regions to have more resources channelled towards creating a more complete recording of not only native species, but also to be introducing and recording more alien species.

Cross-taxon established alien richness. Species-richness values per region varied greatly among taxonomic groups (Fig. 1), making direct calculation of mean cross-taxon alien richness non-informative. Therefore, alien richness was converted to a relative richness scale, ranging from 0 to 1, for each taxonomic group, calculated as the regional species richness divided by the maximum richness for a given taxonomic group. The cross-taxon EAS richness for each region was then calculated as the mean of relative richness values across taxonomic groups. The number of taxonomic groups with data available per region ranged from two (46 regions) to the maximum of eight (145 regions), with a majority of regions (503) having four or more taxonomic groups.

As EAS richness of regions may depend on their area and the level of sampling effort in recording alien species, we also calculated a richness value correcting for these effects. This was achieved by fitting a linear model of ln(cross-taxon EAS richness) as a function of ln(area, km^2), interacting with the sampling effort estimate (both variables were centred on their means and

scaled to their standard deviations). The interaction was included, as an effect of area may be more detectable for regions with greater sampling effort. Indeed, the interaction term was significant and positive (estimate [±SE]= 0.102 [0.030], $F_{1,536} = 11.548$, $P < 0.001$), as were the effects of area (estimate [±SE]= 0.156 [0.033], $F_{1,536} = 15.582$, $P < 0.001$) and sampling effort (estimate [±SE]= 0.178 [0.025], $F_{1,536} = 53.888$, $P < 0.001$) alone. This model explained 13% of variation in cross-taxon alien species richness, and a model that explicitly included the number of taxonomic groups as a weighting yielded very similar results. No regions with zero species across taxonomic groups were included due to a lack of data on sampling effort. The residuals from the non-weighted model were then extracted and used as area- and sampling effort-corrected, cross-taxon EAS richness for mapping and identifying hotspot regions.

Potential drivers of established alien species richness.

We explored the ability of several variables to explain variation in cross-taxon EAS richness and richness of individual taxonomic groups. We calculated gross domestic product per capita (GDPpc) (in US dollars) for each TDWG level 4 region as the average of estimated values in 1 km^2 grid cells, using estimates derived from night time light provided by Ghosh et al[39] . Population density in the year 2000 was calculated in a similar manner from 1 km^2 grid-cell values obtained from the Global Rural Urban Mapping Project (GRUMP; http://sedac.ciesin.columbia.edu/data/set/grump-v1-population-density). Mean annual temperature (MAT) and mean annual precipitation (MAP) were downloaded at 1 minute resolution from WORLDCLIM (www.wordclim.org; mean annual temperature = BIO1, and mean annual precipitation = BIO12 from the bioclim variables), and averages were calculated for each TDWG level 4 region. Area (km^2) was calculated as geodesic area excluding permanent

488 ice-sheets, and each region was classified as being island (including archipelagoes) or mainland
489 (part of a continental landmass; Greenland was coded as an island, Australia was treated as a
490 continental landmass). Distance to mainland was calculated as the geodesic distance to the next
491 continental land mass[40]. Mainland regions were further categorized as being coastal (i.e.
492 bordering seas and/or oceans, not including the Caspian Sea) or landlocked.
493
494 **Analyses.** In order to assess the correlates of cross-taxon EAS richness patterns across all
495 regions, we used linear mixed models using the R package 'nlme'[40] (ln-transformed, to satisfy
496 assumptions of normality of residuals and variance homogeneity) as a function of the following
497 fixed effects: area, sampling effort (average % native species completeness), and area interacting
498 with sampling effort, gross domestic product per capita (GDPpc), population density, mean
499 annual temperature, mean annual precipitation, and whether a region was a mainland or island
500 region. Area, GDPpc and population density were ln-transformed, and mean annual precipitation
501 was square-root transformed to linearize relationships with alien richness. We included the
502 TDWG Level 2 subcontinental regions, nested within TDWG continents as random effects
503 (random intercepts only). We also used the same model as above to model ln-transformed cross-
504 taxon EAS richness for mainland and island regions separately, replacing the mainland-island
505 status with, respectively, a binary variable describing mainland regions as landlocked or coastal,
506 and with distance to the nearest continental landmass (km, square-root transformed) for island
507 regions. We inspected Akaike's Information Criterion corrected for small sample size (AICc) for
508 all full models, and all models nested within them, to identify the set of models within 6 AICc
509 units of the lowest-AIC model that best explain cross-taxon EAS richness for all regions, and for
510 mainland and island regions separately (Supplementary Table 3). The lowest-AICc models

explaining richness across all regions, and for mainland and island regions only, were selected for inference, and marginal R^2 (accounting for fixed effects) and conditional R^2 (accounting for fixed and random effects) were calculated.

For individual taxonomic groups, we also ran linear mixed models as above to explain EAS richness (ln[number of species+1] transformation). Due to insufficient data on sampling effort for several taxa in island regions, we restricted these analyses to mainland regions. Sampling effort for individual taxonomic groups and its interaction with area were included for amphibians, ants, birds, mammals and vascular plants. Sampling effort and its interaction with area was not included in models explaining fish, reptile and spider alien richness because data on native species inventory completeness were not available for these taxonomic groups. Information on model comparisons for individual taxon richness is summarized in Supplementary Table 5.

For all selected models, we checked for spatial autocorrelation of the residuals by constructing correlograms of Moran's *I* in relation to increasing distance (0 to 15000 km) between centroids of neighbouring regions. This was achieved using the 'spline.correlog' function in the R package 'ncf'[42]. To assess significance of spatial autocorrelation, a 95% confidence interval about Moran's *I* was constructed from 500 bootstrapped randomisations of the regions' residuals from the models. For models explaining cross-taxon EAS richness, there was a significant but only small amount of autocorrelation (Moran's $I \leq 0.19$) when all regions or only mainland regions were considered, and only at very short distances between regions (<500 km; Supplementary Fig. 2). For individual taxonomic groups, models showed a significant but small amount of autocorrelation at very short distances for only amphibians (Moran's $I \leq 0.33$,

533 distance ≤ 650 km), birds (Moran's $I \leq 0.23$, distance ≤ 150 km), and freshwater fishes (Moran's
534 $I \leq 0.30$, distance ≤ 750 km) (Supplementary Fig. 3).
535
536 **Congruence in established alien species richness among taxonomic groups.** The strength of
537 correlation in EAS richness between taxonomic groups was assessed by calculating Spearman
538 correlation coefficients for every combination of pairs of taxonomic groups, using the actual
539 species richness for each taxonomic group. The resulting number of regions used per pairwise
540 correlation is shown in Supplementary Table 6. All analyses were conducted in R version 3.2.3[43].
541
542 **Data Availability Statement**
543 The dataset analysed in this study is available in Zenodo data repository,
544 [https://zenodo.org/record/556393#.WPjH08a1s2w].
545
546 **Conflict of Interest Statement**
547 The authors declare that no conflicts of interest have arisen through the production and
548 publication of this article.
549

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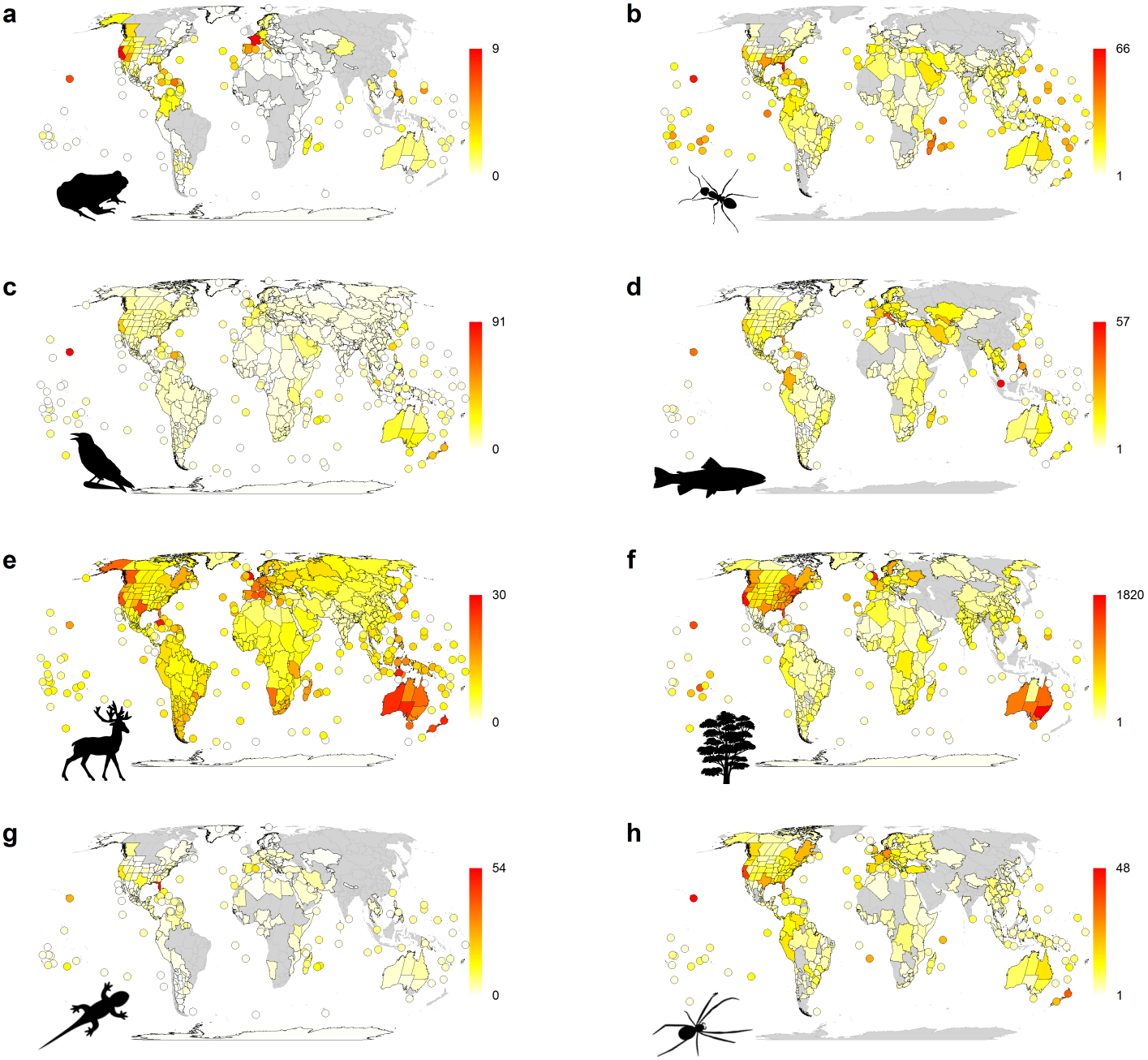
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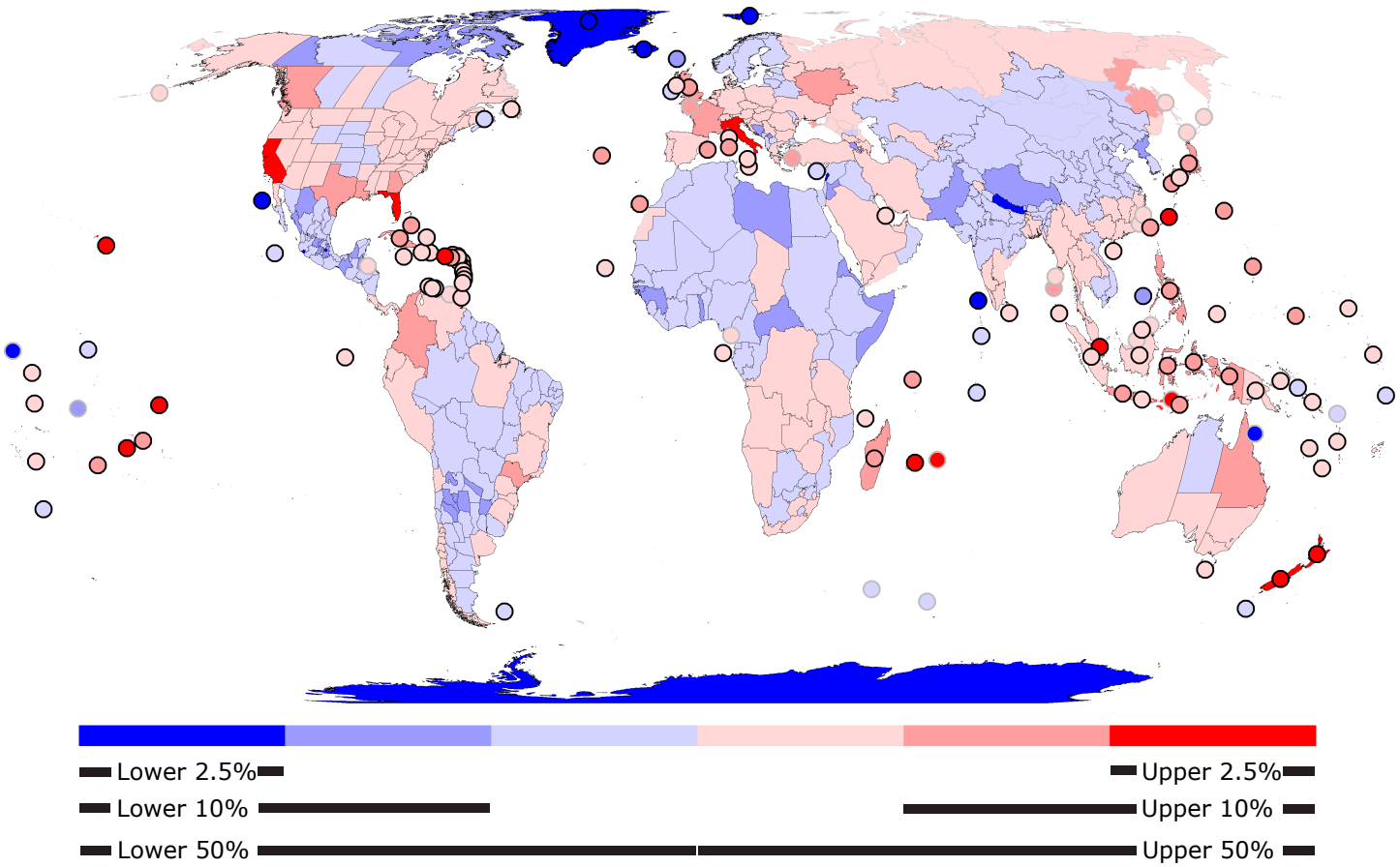
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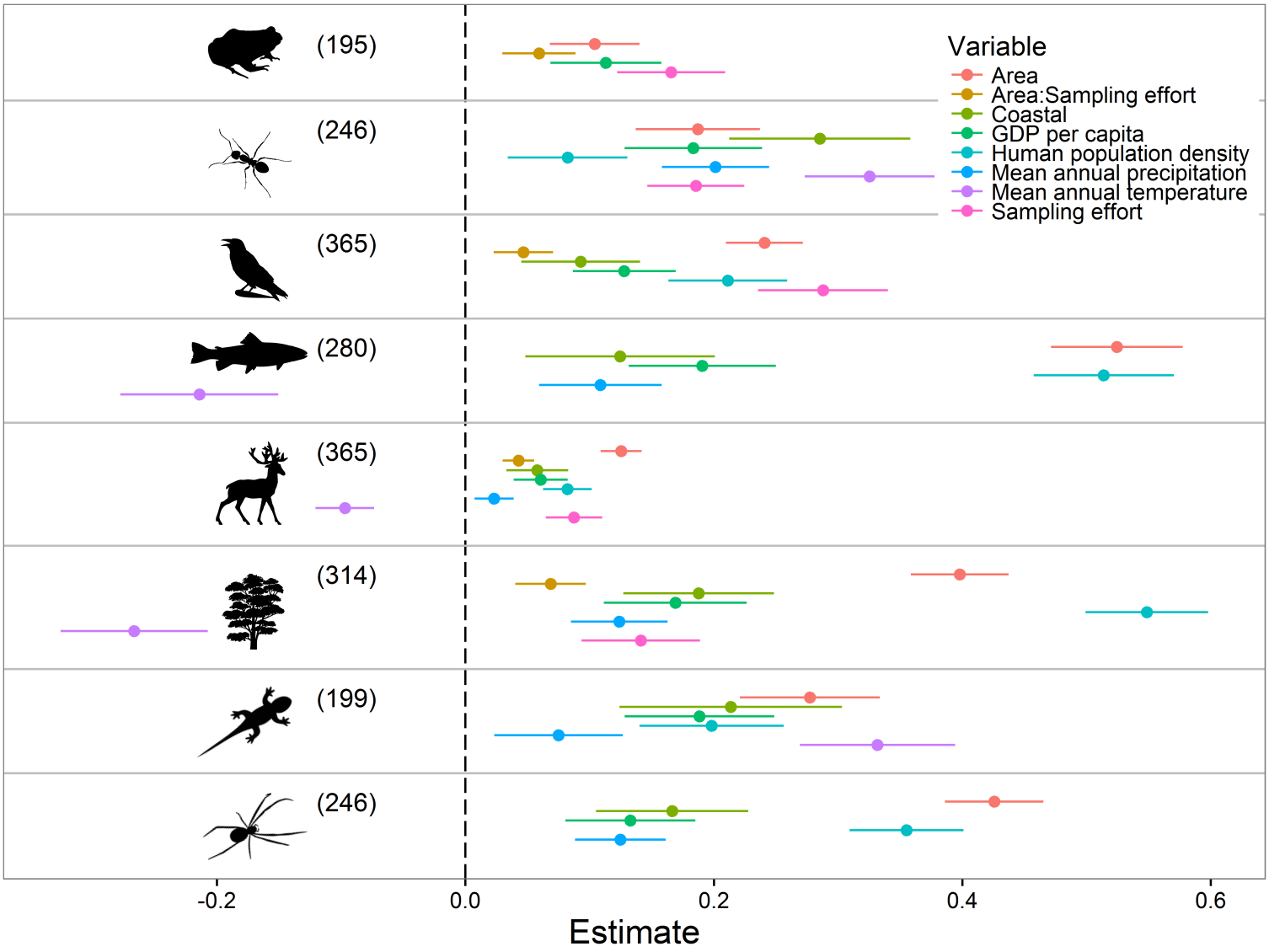
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Variable
Area
Area:Sampling effort
Coastal
GDP per capita
Human population density
Mean annual precipitation
Mean annual temperature
Sampling effort
-0.2
0.0
0.2
0.4
0.6
Estimate